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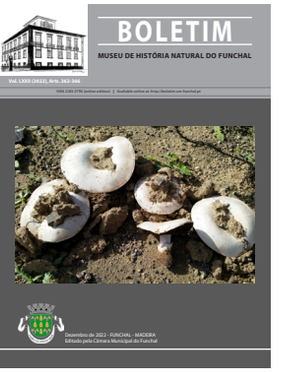

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Unveiling the provenance of cultivated *Taxus baccata* L.(Taxaceae) on the island of Madeira

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With 1 figure and 2 tables

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ABSTRACT: *Taxus baccata* L. (yew) is native to the island of Madeira and wild plants have been shown to belong to a relict lineage, that only exists in Macaronesia. In Madeira, this species has been used as an ornamental plant since at least the 19th century. But, scarcity of native plants, mostly due to over exploitation since the 15th century, which pushed the species to the fringe of extinction, led to the introduction in Madeira of yew plants from Europe. Currently, there are several yew plants in gardens and parks in Madeira, but there are many doubts as to their origin and the possibility of their use in programs for the conservation of the Macaronesian lineage of *T. baccata*. This work aims to clarify the provenance of these yew specimens, through the sequence analysis of the chloroplast *trnS-trnQ* intergenic spacer. All the wild yew plants analysed belong to the Macaronesian haplotype group, whereas all cultivated yew plants in the dataset are consistent with the Euro-Mediterranean lineage and indicative that all these plants are from Continental provenance.

Key words: *Taxus baccata*, relict lineage, cultivated, provenance.

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RESUMO: *Taxus baccata* L. (teixo) é uma espécie nativa da Madeira, pertencendo as plantas selvagens a uma linhagem relíquia, que apenas existe na Macaronésia. Na Madeira, esta espécie é utilizada como planta ornamental pelo menos desde o século XIX. Desde então, a escassez de plantas nativas, principalmente devido à sua sobre-exploração desde o século XV e que levou a espécie à beira da extinção, determinou a introdução na Madeira de plantas de teixo provenientes da Europa. Presentemente existem várias plantas de teixo em jardins e parques ao longo da Madeira, mas existem muitas dúvidas sobre a sua origem e a possibilidade da sua utilização em programas de conservação da linhagem Macaronésica de *T. baccata*. Este trabalho visa clarificar a proveniência desses exemplares de teixo, através da análise de sequências do espaçador intergénico *trnS-trnQ* do ADN cloroplastidial. Os resultados mostram que todas as plantas de teixo selvagens analisadas são do haplótipo Macaronésico, enquanto que todas as plantas de teixo cultivadas são consistentes com a linhagem Euro-Mediterrânica, indicativo de que serão todas de proveniência Continental.

Palavras-chave: *Taxus baccata*, linhagem ancestral, cultivadas, proveniência.

INTRODUCTION

Taxus baccata L. (yew) is a dioecious tree, native to most of Europe, the Atlas Mountains in northern Africa and to the Caucasus Mountains in Asia minor (Benham *et al*., 2016). It is a relic tree species, with fossil records showing its existence during the upper Miocene(0 - 15 million years BP) (Hageneder, 2007), although closely related species have been dated back to the Jurassic period, around 140 million years BP (Hartzell, 1991).

Paleobotanical studies, focusing the Quaternary period (ca. 11.000 years BP), show that, at that time, *T. baccata* populations would have been more abundant and with a wider distribution in Europe than nowadays (Deforce & Bastiaens, 2007). During the late Holocene (from *ca*. 4000-3000 years BP), paleobotanical records indicate a general decline in fossil evidence of *T. baccata*, showing a notable retreat of the yew populations. This decline has been associated to several biological, environmental and anthropic factors, namely climate warming during the Late Holocene and, probably most importantly, exclusive competition with other tree species associated with anthropic activities, such as deforestation, selective felling, grazing and use of wood for tool production (Pérez-Díaz *et al*., 2013).

Presently, *T. baccata* is a declining or even a threatened species in several countries where it is native (Svenning & Magård, 1999; Catarino, 2007; Abella, 2009; Piovesan *et al*., 2009; Katsavou & Ganatsas, 2012; Tumpa *et al*., 2022). The species is rarely found in pure monospecific stands. Instead, it most frequently belongs to diverse forest communities, which, for hosting yew, have been designated as special protection areas by the European Community under the Habitats Directive (92/43/EEC): Mediterranean *Taxus baccata* woods – 9580; Apeninne beech forests with *Taxus* and *Ilex* – 9210; Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrub layer (*Quercion robori-petraeae* or *Ilici-Fagenin*) – 9120 (European Council, 1992; Benham *et al*., 2016).

T. baccata is also native to the archipelagos of Madeira and the Azores. These are part of Macaronesia, a region that includes five north Atlantic archipelagos (Azores, Madeira, Selvagens, Canaries and Cape Verde) and which is included in the Mediterranean basin biodiversity hotspot (Myers, 2000). This region hosts a high number of plant endemics (Jardim & Sequeira, 2008) and encompasses relict plant lineages and species representative of by-gone continental vegetation types, that occurred over Europe during the Tertiary and Quaternary, gone extinct due to sever climate change events during the Quaternary (Vargas, 2007; Fernandez-Palacios *et al*., 2011; Garcia-Verdugo *et al*., 2019).

Recent morphological, ecological, and molecular investigations on Madeiran and Azorean *T. baccata* indigenous plants (Schirone *et al*., 2010; Vessella *et al*., 2013) evidenced several differences from the continental (Eurasian and North African) co-specifics and showed that Madeiran and Azorean yew plants are in fact a relict lineage of the ancestral form of *T. baccata*. These studies point out the need for further studies to assess the evolutionary history and bio-ecology of this lineage and to define an appropriate taxonomic rank for Macaronesian yew lineage.

Unfortunately, in Madeira, as in the Azores, native *T. baccata* is in the fringe of extinction due to over exploitation for timber since the first human settlements in

the 15th century (see Vessella *et al.*, 2013 for a comprehensive account on the historical occurrence and use of wild *T. baccata* in Madeira). In the island of Madeira, although all wild specimens occur within the Natural Park and within two Natura 2000 Network SACs, *i.e.*, "Laurissilva" and "Maciço Montanhoso Oriental", wildfires during the past years have pushed the species even further towards extinction in the wild. Natural populations are currently restricted to a small number of isolated patches, most of them comprising one or few scattered individuals. Despite the rarity of the species, documented since the 19th century (Lowe, 1857, 1862; Taylor, 1882), no information on measures for its recovery is available. During the 20th century, the species was hardly used in forestry recovery programs in Madeira (Campos de Andrada, 1990), probably due to difficulties in propagating the species and the slow growth of the plants (Madeira Forestry Department records).

Despite *T. baccata* having experienced one of the sharpest declines of all European tree species (Benham *et al.*, 2016), for centuries it has been used as an ornamental tree in Europe. The evergreen foliage, red berries, high tolerance to shade and pruning, as well as superstitions and myths built around the species, are some factors that have contributed to this use (Thomas & Polwart, 2003; Catarino, 2007; Abella, 2009). In Madeira, it seems that yew has been used as an ornamental tree since at least the late 19th century (Taylor, 1882). During the 18th century and until the late 19th century, British merchants occupied a pivotal position in the strong growth of the Madeiran economy, as a result of the commodification of Madeiran products, such as wine, real estate and sugar. These wealthy families built or purchased manor houses (*Quintas*), estates of ample proportions which included lawns and beds of exotic plants marked by shade trees, such as oaks, stink-laurel or other less common species (Silva, 2013). Of the latter, yew would have likely fallen into preference, due to its extensive use in Britain as hedging, specimen trees and for topiary. The scarcity of plants of the Madeiran indigenous yew during the late 19th century (Lowe, 1857, 1862; Taylor, 1882; Menezes, 1894) may have led to the introduction in Madeira of yew plants from Europe. This import of plants would have continued during the 20th century, aided by the construction of well-appointed gardens mostly for hotels (Franco *et al.*, 2010) and facilitated by the development of commercial plant nurseries in Madeira. The presence of distinct lineages of yew (Euro-Mediterranean and Macaronesian) in Madeira has been showed by Vessella *et al.* (2013). According to these authors, although plants from Madeiran provenance show peculiar leaf size and morpho-anatomical characters, distinguishing them from Continental provenance ones, based on morphological characters, is still complex.

Presently, several plants of *T. baccata* can still be found in several manor house (*Quintas*) gardens, public gardens (Quintal, 2007), roadsides and even in forest parks in Madeira. Their location, in reference to the native plants' location and habitat, suggests that they were most likely introduced by man, but there are many doubts regarding the provenance of these cultivated plants, whether they are native or introduced. In almost all cases, no historical records on the provenance of the plants exists.

The scarcity of known Madeiran *T. baccata* plants and its high risk of extinction calls for urgent conservation measures. The lack of wild plants and seed availability may lead to collecting yew plant material for propagation where it is easily available, such as gardens and forest parks. Given the difficulties to distinguish between plants of the Macaronesian and Euro-Mediterranean lineages, it is of utmost importance that the origin of the cultivated plants is determined, and thus avoid crossbreeding and assuring the conservation of the Macaronesian lineage. This study aims clarifying the provenance of the cultivated yew specimens in Madeira and contribute to the conservation of the Macaronesian lineage of *T. baccata*.

MATERIAL AND METHODS

Cultivated *T. baccata* plants' lineage was assessed through DNA sequence analysis of the chloroplast *trnS–trnQ* intergenic spacer, located in the large single-copy region of the plastid genome, between trnS and trnQ coding regions. This marker was used for the first time by Hao *et al.* (2008), who found it able to discriminate among 14 Old World and New World *Taxus* species. The primers used in this study were designed and used by Schirone *et al.* (2010) to detect the persistence of an ancient Macaronesian yew lineage in the Azores, and further used by Vessella *et al.* (2013) to detect that same lineage in Madeira.

For this study, leaf samples from all *T. baccata* plants in private and public gardens in Madeira (Fig. 1 and Table 1), as well as of wild plants from most known populations, were collected, dried in silica gel and stored at -5 ºC prior to DNA extraction. Herbarium voucher specimens were produced and deposited in the MADJ herbarium (herbarium acronym according to Thiers, 2022). Leaves were homogenized using TissueLyser II from QIAGEN. Total genomic DNA extracts were obtained by using GeneJET

Plant Genomic DNA Purification Mini Kit following the manufacturer's instructions. Amplification using plastid *trnS–trnQ* DNA marker followed the procedure described by Schirone *et al*. (2010). Representatives of *T. baccata* from adjacent areas (Mediterranean Basin, North and Central Europe), as well as from the Madeiran and Azorean haplotype, referenced by Schirone *et al*. (2010) and Vessella *et al*. (2013) and available in NCBI Database, were also included in the dataset to establish a reference for comparison (Table 2). Sequences were analysed and aligned using MEGA7.

RESULTS AND DISCUSSION

The alignment includes a set of 43 *T. baccata* sequences; 36 novel and 7 extracted from NCBI database. The novel includes 28 cultivated yew plants from 16 locations and wild plants from 8 distinct locations in the island of Madeira (Table 2).

The cpDNA sequences in the dataset showed two polymorphic sites, one in the position 486 (T/G) and another in position 596 (A/G) (Table 2), consistent with the results described by Schirone *et al*. (2010) and Vessella *et al*. (2013). According to these authors, samples sharing the same nucleotide substitutions can be clustered into two groups: one including Madeiran and Azorean wild plants and another including Euro-Mediterranean *Taxus baccata* (see Table 2; sequences 1 and 2 – Macaronesian haplotype and sequence 11 to 15 – Euro-Mediterranean haplotype).

All the Madeiran wild yew plants tested in this study fell into the Macaronesian haplotype group. On the other hand, all cultivated yew plants in the dataset (samples 16 to 43) showed the same sequence and substitutions, consistent with the Euro-Mediterranean lineage and indicative that all these plants are from Continental provenance. Based on the size of the plants and information gathered from personnel working in the gardens, most of these plants were probably planted during the end of the 19th century and first half of the 20th century.

Special awareness should be directed to the yew plant samples 36 to 43, especially those located at the "Casa de Abrigo do Pico Ruivo" and "Posto Florestal da Boca da Corrida". These plants, all tested as from Euro-Mediterranean lineage, are in or near the Natural Park of Madeira and in some cases close to extant wild plants of *T. baccata*, located on nearby cliffs. In these areas, where natural vegetation is mostly a transition between "Madeiran laurisilva" to the "Madeiran cloud heaths", regeneration of indigenous yew plants may occur, without being noted due to the very rugged terrain and steep cliffs. Considering this proximity of plants of the two distinct lineages, the possibility of crossbreeding between them cannot be excluded, especially considering the anemophilous pollination of yew. Male plants freely expel a myriad of pollen grains specialized for long distance transportation by wind, estimated up to 700 m (Chybicki & Oleksa, 2018).

The yew plants located in the two Governmental Forest Department nurseries: "Viveiro Florestal do Pico das Pedras" and "Viveiro Florestal da Casa Velha", were also shown to belong to the Euro-Mediterranean lineage. The presence or removal of these plants should be adequately addressed, as these nurseries are the main areas in Madeira for propagation of plants of several species for conservation purposes, including yew.

The indigenous *T. baccata* plants are scarce and seriously threatened by extinction. In August 2010, a wildfire severely affected the wild yew populations and habitat, leading to the loss of around 30 of the 61 known plants. Since then, new yew plants have been found, but the total number is still less than 50, critically low and inadequate for the long-term survival of the species in Madeira (IUCN, 2012). Although the best strategy to conserve this lineage is *in situ* conservation through preservation of the natural habitat, wildfires are still a major threat, very unpredictable and difficult to address, especially when considering the island's topography. Thus, the recruitment of new plants must have high priority, with reinforcement of populations and reinstallation of plants over a broad array of locations, particularly in those where yew is known to have occurred in the past. This recruitment should also consider tackling possible genetic processes, in action due to reduced population size and severe fragmentation that may act as an additional limiting factor for the recovery of the species.

Maintaining plants of endangered species in gardens or parks is an important and valid conservation measure (Borsh & Lohne, 2014). At the least, the cultivated plants are an important source of seeds or other plant material necessary for propagation. But only well documented plants are adequate sources for scientific research as well as *ex situ* or *in situ* conservation programs (Rae, 2011). It is expected that the data brought here will contribute to the awareness of this circumstance and contribute to the development of a conservation strategy for the Macaronesian yew.

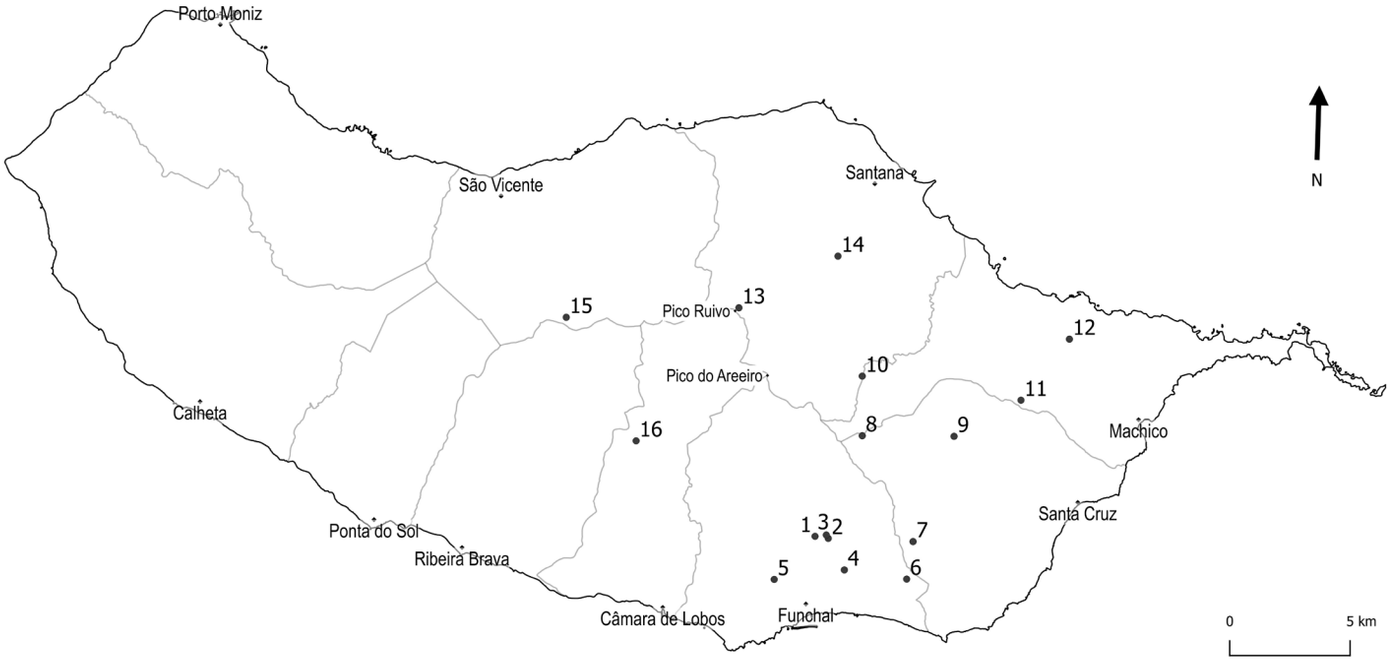

Fig. 1 – Madeira Island. Each numbered point indicates the location of cultivated *T. baccata* plants analysed in this work. See Table 1 for description of location number.

Table 1 – Location and number of cultivated *T. baccata* plants sampled. The numbers for each location match the numbers on Fig. 1.

Number in Map (Fig.1)	Location	Number of Plants
1	Jardim do Imperador	1
2	Quinta Monte Palace	3
3	Jardim Municipal do Monte	1
4	Jardim Botânico da Madeira Eng.º Rui Vieira	3
5	Jardim do Tecnopolo	1
6	Quinta do Palheiro Ferreiro	3
7	Quinta do Padre Américo	4
8	Posto Florestal do Poiso	1
9	Viveiro da Casa Velha	1
10	Parque Florestal do Ribeiro Frio	1
11	Quinta do Santo da Serra	2
12	Parque Florestal das Funduras	1
13	Casa de Abrigo do Pico Ruivo	3
14	Viveiro Florestal do Pico das Pedras	1
15	Posto Florestal da Encumeada	2
16	Posto Florestal da Boca da Corrida	1

Table 2 – Relevant positions in the alignment of the chloroplast *trnS–trnQ* spacer sequences that differentiate Macaronesian and Euro-Mediterranean haplotype of *T. baccata*. Black arrows indicate polymorphism in positions 486 and 596. Wild group corresponds to Madeiran native plants sampled for this analyses. Cultivated group indicates cultivated plants sampled for this study. GenBank sequences – NCBI group (Accession code in brackets) serve as reference for comparison.

Name	Group	483	484	485	486	487	488	489	490	491	593	594	595	596	597	598	599
1. Azores_Pico Island (GU320044.1)	NCBI	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
2. Madeira_haplytype (JN255689.1)	NCBI	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
3. Sao Vicente (F48)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
4. Boaventura (U37)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
5. Curral-das-Freiras (C83)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
6. Santana (V58)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
7. Santana (N41)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
8. Santana (T63)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
9. Santana (Q27)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
10. Santana (L36)	Wild	C	C	A	G	A	A	T	A	G	A	T	G	G	A	A	A
11. Continental_haplotype (JN255688)	NCBI	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
12. United Kingdom_Wales (GU320039.1)	NCBI	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
13. Spain_Font Roja (KP115931.1)	NCBI	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
14. Italy_Sardinia (GU320034.1)	NCBI	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
15. Morocco (GU320038.1)	NCBI	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
16. Jardim do Tecnopolo	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
17. Jardim do Imperador	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
18. Jardim Municipal Monte	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
19. Quinta Monte Palace_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
20. Quinta Monte Palace_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
21. Jardim Botanico da Madeira_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
22. Jardim Botanico da Madeira_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
23. Jardim Botanico da Madeira_3	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
24. Quinta do Palheiro Ferreiro 1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
25. Quinta do Palheiro Ferreiro 2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
26. Quinta do Palheiro Ferreiro 3	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
27. Quinta do Padre Americo_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
28. Quinta do Padre Americo_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
29. Quinta do Padre Americo_3	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
30. Quinta do Padre Americo_4	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
31. Posto Florestal do Poiso	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
32. Viveiro Florestal da Casa Velha	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
33. Quinta do Santo da Serra_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
34. Quinta do Santo da Serra_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
35. Parque Florestal das Funduras	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
36. Parque Florestal do Ribeiro Frio	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
37. Viveiro Florestal do Pico das Pedras	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
38. Casa de abrigo do Pico Ruivo_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
39. Casa de abrigo do Pico Ruivo_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
40. Casa de abrigo do Pico Ruivo_3	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
41. Posto Florestal Encumeada_1	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
42. Posto Florestal Encumeada_2	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A
43. Posto Florestal da Boca da Corrida	Cultivated	C	C	A	T	A	A	T	A	G	A	T	G	A	A	A	A

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